AN ABNORMAL SPECIMEN OF THE SILURIAN ANOMALOCYSTITID MITRATE *PLACOCYSTITES FORBESIANUS*

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ABSTRACT. An unusual specimen of the Silurian anomalocystitid mitrate *Placocystites forbesianus* is described. Unlike the normal morphology of the species, the anterior, transverse row of ventral plates consists of two rather than three elements; the mid-ventral plate of the next posterior transverse row is reduced in size and wedged between the lateral elements of the same row; the plate arrangement on the anterior half of the ventral skeleton is asymmetrical; the left lateral and admedian ventral plates are smaller than the corresponding plates of the right side; finally, the placocystid plate has a slightly pronounced anterior angle. The abnormal skeletal features of this specimen are interpreted as a developmental response to the absence of an anterior ventral plate.

ABNORMAL plating patterns in representatives of the extinct group known as the mitrates have been documented so far only in the peltocystid *Peltocystis cornuta* Thoral, 1935 and, possibly, in the anomalocystitid *Ateleocystites huxleyi* Billings, 1858. Several specimens of *Peltocystis* show an inverted arrangement of the dorsal and ventral head plates (Ubaghs 1968, 1969; Jefferies 1986, 1991; Jefferies *et al.* 1996). This condition is known as *situs inversus*. Jefferies (1991) suggested that *Peltocystis* probably possessed an echinoderm-like larva that could attach to the substrate with either its left or its right side. An analogous behaviour is documented in some pleuronectiform fishes. A single specimen attributed by Wright *et al.* (1977) to *Ateleocystites huxleyi* was reported as having an extra ventral head plate lying immediately anterior to the placocystid plate, or plate V17 (see below) (Kolata and Jollie 1982; Parsley 1991).

In this paper, an abnormal specimen of the anomalocystitid *Placocystites forbesianus* de Koninck, 1869 is described (Text-fig. 1A–B). Jefferies and Lewis (1978) provided a thorough account of the external and internal anatomy of this mitrate, and discussed extensively its craniate affinities. Savazzi *et al.* (1982) and Jefferies (1984) elaborated on its functional morphology and showed that, like other mitrates, *Placocystites* probably moved rearward within mud, pulled by its tail (see also Savazzi 1994). The preliminary results of a comprehensive cladistic analysis of the anomalocystitids carried out by the author show that *Placocystites* is closely related to *Rhenocystis latipedunculata* Dehm, 1932 and *Victoriacystis wilkinsi* Gill and Caster, 1960 (Parsley 1991; Ruta 1997). In these three species, three large plates occupy a sub-central or slightly anterior position on the ventral head skeleton.

The ventral plate nomenclature used in this paper (Text-fig. 1D) follows Ruta and Theron (1997). The dorsal plate nomenclature (Text-fig. 1C) is simplified with respect to both Jefferies and Lewis's (1978) and Ruta and Theron's (1997) systems, and is based on a revised terminology of the anomalocystitid skeleton which will be discussed elsewhere. The anatomical interpretation and morphological orientation of *Placocystites* follow the works of Jefferies and Lewis (1978) and Jefferies (1986). Throughout, the term 'normal individuals' implies reference to typical individuals of *Placocystites forbesianus*.
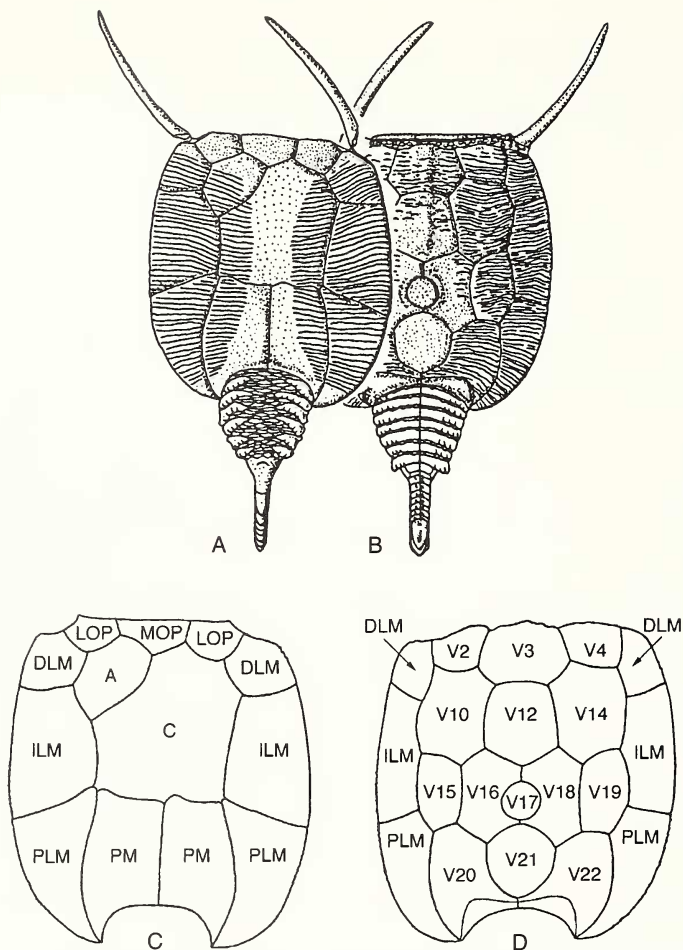
TEXT-FIG. 1. Reconstruction of *Placocystites forbesianus* de Koninck, 1869. A, dorsal view; B, ventral view; C, nomenclature of the dorsal head plates; D, nomenclature of the ventral head plates. In C and D, the sculpture of the skeleton is omitted (A and B redrawn and modified after Jefferies and Lewis 1978; C and D redrawn and modified after Jefferies 1986).
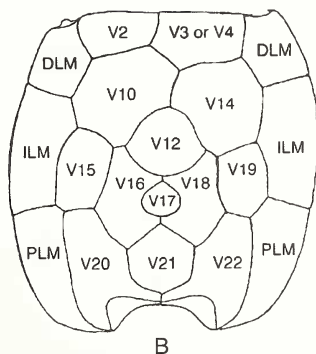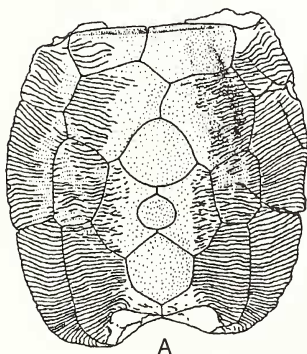
Anterior

Left   Right   Left

A   B

Posterior

TEXT-FIG. 2. *Placocystites forbesianus* de Koninck, 1869; Dudley Limestone, England; specimen HC11; Holcroft Collection, Lapworth Museum, University of Birmingham. A, dorsal head skeleton; B, ventral head skeleton. Both × 2.

Anterior

Right   Left

A   B

Posterior

TEXT-FIG. 3. *Placocystites forbesianus* de Koninck, 1869; Dudley Limestone, England; specimen HC11; Holcroft Collection, Lapworth Museum, University of Birmingham. A, camera lucida drawing, ventral view; B, ventral plate nomenclature. Scale bar represents 10 mm.

MATERIAL AND METHODS

The abnormal specimen of *Placocystites* was collected from the Dudley Limestone (Wenlock age; see Jefferies and Lewis 1978 and references therein for an account of the stratigraphy), and is conserved in the Lapworth Museum, University of Birmingham (Holcroft Collection, no. 11). Henceforth, it will be referred to as HC11. This specimen was mentioned, but not figured, by Jefferies and Lewis (1978), who made no reference to its peculiar ventral plating pattern in their work. It consists of an almost complete head, only slightly disrupted dorsally, and some proximal fore tail rings (Text-fig. 2). Although the oral spines are missing, the right plate DLM shows a toroidal tubercle for the articulation of the right oral spine (see also Jefferies and Lewis 1978, pl. 1, figs 37–39; pl. 2, figs 47–49, 54–55).

HC11 was originally partly embedded in a piece of greenish silty marl. Most of the ventral head skeleton was completely exposed. The embedding material was wetted with water and removed with a needle. More resistant material, in the form of layers of iron oxide, was partly removed with the aid of an air-abrasive machine using a soft abrasive (sodium bicarbonate). Ultrasonic cleaning was used to wash off most of the residual sediment. The specimen was drawn in ventral view using a *Camera lucida* (Text-fig. 3A).

DESCRIPTION

Only the ventral head skeleton (Text-fig. 2B) is described, since the dorsal skeleton (Text-fig. 2A) does not show abnormal features. The description is best understood by reference to the ventral plating pattern of a normal individual (Text-fig. 1D). Throughout, 'left' and 'right' refer to the animal, not to the observer.

The most remarkable asymmetries of HC11 are in the anterior half of the ventral head skeleton (Text-figs 2B, 3; Pl. 1, fig. 3). In normal individuals, three large polygonal plates are present just anterior to V15–V19 (Text-fig. 1B, D). By comparison with the Lower Devonian *Bokkeveldia oosthuizeni* Ruta and Theron, 1997, these three plates are labelled from right to left (with respect to the animal) as V10, V12 and V14. In *Placocystites, Rhenocystis* and *Victoriacystis*, V10 and V14 are mirror images of each other. In *Placocystites*, V12 is as large as or slightly smaller than either V10 or V14. In HC11, the three plates present immediately anterior to V15–V19 (Text-figs 2B, 3; Pl. 1, fig. 3) appear to be homologous to V10, V12 and V14, on the basis of their mutual contacts and with reference to their position with respect to the surrounding elements (Text-figs 1D, 3B). However, the relative proportions of the sutures formed by V10 and V14 with the adjacent plates differ significantly from those found in normal individuals. The suture between V10 and V14 lies anterior to V12 and bends strongly leftward, although its anteriormost extremity is slightly concave towards the right (Text-figs 2B, 3; Pl. 1, fig. 3). V12, approximately equal in size to V21 and tightly wedged between V10 and V14 (Pl. 1, fig. 3), shows three margins. Its posterior margin is semi-elliptical and forms an angle of about 120° with each of the two antero-lateral margins; these are mostly convex outward, and meet along the ventral midline, likewise forming an angle of 120° (Text-figs 2B, 3). Normally, V12 is sub-pentagonal and slightly longer than wide (Jefferies 1984), and its anterior margin is either concave posteriorly or chevron-shaped (Text-fig. 1B, D).

PLATE 1

RUTA, *Placocystites*

Anterior to V10, V12 and V14 are two plates of unequal size (Text-figs 2B, 3; Pl. 1, fig. 3). The smaller, right plate is four-sided; the larger, left plate is five-sided. Both plates show a shallow groove running along their anterior margins; in life, this groove gave insertion to a flap of integument connected with the oral plates (Jefferies and Lewis 1978, pl. 2, figs 54–55). The right plate probably corresponds to V2. As in other specimens of *Placocystites*, this plate contacts the ventro-lateral extension of the right DLM, laterally, and V10, posteriorly. Unlike the normal condition, V2 is much wider than long, and the median ends of its anterior and posterior margins are closer to each other than the lateral ends. The identification of the left anteriormost plate poses some problems. If the head of HC11 is held resting on its dorsal face, the external surface of the left anteriormost plate shows two almost planar, outward-sloping areas somewhat like the roof of a house. These areas meet approximately in the centre of the plate forming a rounded, antero-posterior 'gable'. The latter runs in a slightly oblique direction on the anteriormost part of the external surface of V14, where it disappears gradually (Text-fig. 3A; Pl. 1, fig. 3). In normal individuals, the anterior third of the ventral skeleton likewise shows two sloping areas and the 'gable' occupies the central part of the external surface of V3 and, in part, V12 (Text-fig. 1B,). In HC11, the left anteriormost ventral plate may, therefore, correspond to V3. The median half of the suture between V14 and the presumed element V3 is concave rearward, whereas its lateral half is concave forward. Alternatively, this element could correspond to a medially expanded plate V4 (Text-fig. 1B, D). In normal specimens, V4 is a four-sided element in contact with the ventro-lateral extension of the left DLM, laterally, and with V14, posteriorly. On the basis of the available evidence, I tentatively identify the left anteriormost plate of HC11 as V3.

The relative proportions of the plates on the posterior half of the ventral skeleton of HC11 (Text-figs 2B, 3) differ slightly from those in normal specimens. V22 is slightly narrower and shorter than V20, whereas in other specimens, V20 and V22 are mirror images of each other (Text-fig. 1B, D), and their shape changes only slightly during ontogeny (Jefferies 1984, fig. 9). In HC11, and in some adult individuals of *Placocystites*, V21 is roughly hexagonal and almost as long as wide (Text-figs 2B, 3; Pl. 1, fig. 2). In some specimens, such as BMNH E7588 (Jefferies and Lewis 1978, pl. 4, fig. 72), all the sides meet at obtuse angles. However, in most specimens (such as HC35; Jefferies and Lewis 1978, pl. 1, fig. 41), the two antero-lateral sides of V21 are replaced by an anteriorly convex margin. In young individuals of *Placocystites*, V21 is rhomboidal to roughly elliptical in outline and is in contact with V17 anteriorly (see Jefferies 1984, fig. 9); in addition, its postero-lateral sides are convex externally. The latter condition is also observed in adults of *Ateleocystites guttenbergensis* (Kolata and Jollie 1982) and *Barrandeocarpus jaekeli* (Ubaghs 1979), and may represent a primitive feature for the anomalocystitids, as suggested by a recent unpublished cladistic analysis of this group carried out by the author. The ontogenetic changes of V21 in *Placocystites* probably recapitulate the modifications undergone by this plate in the evolutionary history of a clade of mitrates which is mainly represented by boreal forms.

V15–V19 in HC11 do not differ significantly from the normal condition in *Placocystites*, except that V19 is smaller than V15, and V16 is only slightly larger than V18 (Text-figs 2B, 3). The suture between the ventro-lateral extension of the right plate ILM and V15 is much longer than the suture between the same plate and V10. Conversely, the two sutures formed by the ventro-lateral extension of the left ILM with V14 and V19 are sub-equal in length (Text-figs 2B, 3). In addition, the suture between the ventro-lateral extension of the right PLM and V15 is much shorter than its counterpart on the left side. V16 and V18 surround plate V17 and meet mid-ventrally forming two sub-equal, short sutures in front of and behind this plate (Text-figs 2B, 3; Pl. 1, fig. 1). V17 possesses a slightly pronounced anterior angle (in other specimens, this plate is smoothly curved). The anterior margins of V15 and V19 lie in front of the anterior margins of V16 and V18 respectively (Text-figs 2B, 3), whereas in normal individuals, V15, V16, V18 and V19 form a transverse row (Text-fig. 1D).

Ventral sculpture. Transversely elongate, terrace-like ridges (cuesta-shaped ribs of Jefferies 1986) are present on the ventro-lateral extensions of DLM, ILM and PLM, as well as on V10, V14, V15, V16, V18 and V19 (Text-figs 2B, 3A). A few irregular ridges are also present near the right margin

of V2. In V16 and V18, they occupy the lateral half of each of these two plates and are irregular, tending to form a reticulate pattern and breaking up in a median direction. This morphology is also observed along the most median part of the ornamented area on V10 and V14. In normal individuals, the ridges (both dorsal and ventral) usually terminate abruptly in a median direction. In HC11, the external surfaces of V3, V12, V17 and V21 are smooth (Jefferies 1984).

Stereom. Traces of stereomic structure, in the form of closely spaced perforations of various shapes and sizes, are widely distributed on the unribbed regions of the ventral skeleton of HC11, where they form irregular patches separated by more compact calcite, as well as on the most median parts of the ribbed areas (Text-fig. 2B, 3A; Pl. 1, figs 1–3). The stereom structure is visible only externally, and it is, therefore, impossible to ascribe it to any particular morphological category based on the three-dimensional arrangement of trabeculae and canals (Smith 1980). The rearmost third of the gentle slope of the ventral terrace-like ridges likewise shows minute perforations, which are on average smaller than those on the unribbed areas.

DISCUSSION

The development of the anomalocystitid skeleton, like that of other calcite-plated animals, cannot be understood by examining the fate of individual plates in isolation. As pointed out by Raup (1968, p. 53) in his theoretical study of plate growth in echinoids, '… one must look upon the total skeleton as a product of the development of the plate mosaic'. Raup discussed the morphological features observed in the echinoid test in terms of plate close-packing interaction. He explained the behaviour of the interacting plates by analogy with that of soap bubbles in contact with each other. Jefferies (1984) extended Raup's arguments to the plate development in *Placocystites*. Here, I shall try to explain the abnormal features of the ventral skeleton of HC11 on the basis of the theoretical model discussed by Raup (1968) and Jefferies (1984). A major limitation is imposed by the fact that growth lines are not preserved in HC11. Therefore, it is not possible to assess the relative rates at which individual plates grew in different directions and to detect their morphological modifications during the ontogeny of HC11.

The most distinctive feature of HC11 is the absence of a ventral plate (perhaps V4; see above) from the anteriormost transverse row. This absence probably results from the suppression of the centre of calcification pertaining to that plate, although it is impossible to establish which factor (or factors) might have caused this suppression. The relative and absolute size of the remaining two plates of the anteriormost row is greater than in normal individuals, presumably because they developed without the spatial constraints imposed by the third element. The modifications of V2 and V3 perhaps caused a medianward displacement of the antero-median angle of V10.

I hypothesize that the ventral plates of HC11 developed at an unusually fast rate, and that the growth rate of the anterior ventral elements was much greater than that of the posterior ventral plates. A comparison with other individuals of *Placocystites* (see, for example, Jefferies 1984, fig. 9) shows that V2, V3, V10 and V14 in HC11 are larger than V15–V19 (compare Text-figs 2B, 3 with Text-fig. 1). Early in the ontogeny of HC11, growth rate might have been higher near the left anterior angle and along the anterior margin of the ventral skeleton, and progressively lower in an antero-posterior direction. The asymmetrical arrangement of V10 and V14 can be explained as a result of differences in development rate on the right and on the left of the longitudinal axis of the head. V19 and V22 were perhaps only partially influenced by the fast development of the anterior plates, whereas V15 and, in part, V20 may have been characterized by a more rapid growth, presumably as a consequence of the slight anterior displacement of V10.

Two independent lines of evidence support the proposed developmental scenario. The first comes from the distribution of the ventral sculpture. As discussed previously, V3, most of V2, V12 and the area lying just anterior to V12 are externally smooth. In other specimens, the anterior part of the external surface of V12, as well as plates V2–V4 are sculptured. Jefferies (1984, fig. 9) showed that the ventral ridges first appeared posteriorly during ontogeny, and eventually spread forward. Also,

ridges were short and irregular early in development, but became confluent and straightened as the head grew. In HC11, the presence of a relatively large, smooth anterior area may be explained in terms of the rapid growth of the anterior ventral plates. Fast growth might have required a rapid allocation of calcite; the mesenchyme involved in the formation and deposition of ridges could have provided an additional source of skeletal material. Therefore, the relatively fast development of the plates might have implied a suppression or a retardation of the deposition of the terrace-like structures.

The second line of evidence favouring relatively rapid growth is the presence of stereomic structure. HC11 is unlikely to represent an immature specimen, as its size is comparable to that of the largest recorded individuals of *Placocystites*. Also, the smallest known individuals of this mitrate do not show any stereom structure, their plates being composed of compact calcite (Jefferies and Lewis 1978). On the basis of these observations, I conclude that the plates of HC11 are probably incompletely calcified in places, and that deposition of calcite occurred irregularly, probably as a result of the unusually rapid development.

The two mid-ventral elements V17 and V12 deserve further comment. In his analysis of the external ontogenetic changes in *Placocystites*, Jefferies (1984) provided a detailed account of the most distinctive features of V17 (called by him *xi*), or the 'placocystid plate' (Caster 1952). These are summarized as follows: V17 is always smooth-surfaced; in the largest specimens, it is in contact with V16 and V18 only, whereas in the smallest individuals it forms sutures with V21 and V12 as well; its size is independent of that of the head; its outline is always smoothly curvate, never sharply angular; the sutures between this plate and the surrounding elements slope ventralward and outward, so that the internal surface of V17 is much smaller than the external surface. These observations led Jefferies (1984) to hypothesize that V17 probably ceased growing early in ontogeny, reached its final size well before other plates started pushing against it, and thereafter had a limited capacity of adding material to its inner surface. In HC11, V17 has a slightly pronounced anterior angle. This suggests that V16 and V18 probably began to press against V17 before the last had attained its final size. The angles formed at the triple junction between V16, V17 and V18 measure 120° each. The interaction of V17 with V16 and V18 probably started just antero-lateral to V17; after V17 was fully developed, V16 and V18 perhaps continued to grow, mainly in a posterior and median direction.

The external margin of V12 shows angles mid-anteriorly and laterally, but not posteriorly. Unlike V17, V12 probably interacted with the surrounding plates throughout its growth. This is deduced from the fact that the angles formed at the triple junctions between V12 and each of the plates with which this element is in contact measure 120°. The available evidence suggests that the development of V12 was severely limited anteriorly by the interaction with V10 and V14. Such interaction would explain the presence of externally convex antero-lateral margins. In a close-packing model of interaction (Raup 1968), the margins of smaller plates are convex towards the larger plates. The presence of a convex posterior margin in V12, on the other hand, probably accounts for a relatively rapid development of this plate in a posterior direction, with modalities of growth similar to that of V17.

A final note concerns V21. In several mitrates (such as *Anomalocystites*, *Ateleocystites*, *Barrandeocarpus*, *Bokkeveldia*, *Rhenocystis* and *Victoriacystis*), V21 often shows externally convex margins. Unlike V17, V21 probably started interacting with the surrounding elements before it had reached its final size, and was capable of rapid growth even when in contact with the adjacent plates. Therefore, the trade-off between close-packing interaction with the posterior ventral plates and early, rapid development may explain why in some specimens of *Placocystites* (including HC11) V21 is neither precisely polygonal nor rounded.

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